THE UNEXPECTED OCCURRENCE OF ALEURONE COLORS IN F_2 OF A CROSS BETWEEN NON-COLORED VARIETIES OF MAIZE

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BEFORE the Mendelian methods of analysis became available, considerable wonder would doubtless have been excited by the "mysterious" appearance in F_2 of one colored grain—purple or red—to every five or six white ones in case of a maize cross, both parents and F_1 of which had only white grains. An occurrence of this sort has recently been noted in one of my maize cultures and the F_2 numbers are explained here as a trihybrid or tetrahybrid ratio. The crosses in question were made primarily for a study of size inheritance and fairly large numbers have been grown. The varieties concerned are two dwarfs of distinctly different types, Tom Thumb pop and California Rice pop, and a tall type Missouri dent. The facts with reference to aleurone color are these: Tom Thumb pop, a "white" corn (*i. e.*, having non-colored aleurone), was crossed with Missouri dent, also a white corn. Three generations of hybrid plants—four generations for aleurone and other endosperm characters—have been grown without the appearance of any but white grains. The same white-seeded Missouri dent was also crossed with the white-seeded California pop. The three hybrid generations grown to date have shown no aleurone color. Furthermore, when the same white Tom Thumb pop was crossed with the same white California pop, only white grains appeared in F_1. But both of the two ears containing F_2 seeds—the only ones that have been produced as yet—had a sprinkling of both purple and red grains, too many to be explained as due to care-

less guarding against foreign pollen and too few to be accounted for by any simple monohybrid or dihybrid formula. The actual numbers of grains of the various sorts were as follows:

Ear 1	43 purple, 10 red, 308 white.
Ear 2	32 purple, 11 red, 222 white.
Total	75 purple, 21 red, 530 white.

The fact is familiar that in crosses of purple with white varieties of corn, there often appear in addition to the monohybrid ratio of three purple grains to one white one, purple, red and white grains in the dihybrid ratios of 9:3:4 (East and Hayes[1] and Emerson[2]). It is also well known that in similar crosses purple and white grains may appear in F_2 in the reversed monohybrid ratio of 1:3 or the dihybrid ratio of 9:7 (East and Hayes[1]). East[3] has recently shown that for the production of purple aleurone there must be present three Mendelian factors, *C, R,* and *P,* and has demonstrated for purple, red, and white grains the trihybrid ratio of 27:9:28. *C* is a general color factor, that must be present ordinarily in order that any color may develop, *R* a factor that has to do with the production of red aleurone when *C* is present, and *P* a factor for purple that is effective only in the presence of both *C* and *R*. Thus *CRP* gives purple and *CRp* red, while all the other possible combinations give white. All this is on the assumption that a fourth factor *I,* an inhibitor of color development, is absent. Purple color of the aleurone may, therefore, be said to depend upon the presence of three factors and the absence of one, *CRPi,* red color upon the presence of two factors and the absence of the two others, *CRpi,* and whites upon the absence of either one of the two factors *C* or *R* or upon the presence of a third factor, *I, cRP, CrP,* or *CRPI,* etc.

[1] E. M. East and H. K. Hayes, Conn. Agr. Expt. Sta., Bul. 167, pp. 57–100, 1911.

[2] R. A. Emerson, Amer. Breeders' Assoc., vol. 6, pp. 233–237, 1911.

[3] E. M. East, AMER. NAT., vol. 46, pp. 363–365, 1912.

If the numbers obtained in F_2 of the cross of Tom Thumb pop with California pop are to be regarded as constituting a tetrahybrid ratio, all four aleurone factors must be heterozygous in F_1 the formula being *CcRrPpIi*. The F_2 generation would then be constituted as follows:

27 *CRPi*	27 purple
9 *CRpi*	9 red
9 *CrPi* 9 *cRPi* 3 *Crpi* 3 *cRpi* 3 *crPi* 1 *crpi* 81 *CRPI* 27 *CRpI* 27 *CrPI* 27 *cRPI* 9 *CrpI* 9 *cRpI* 9 *crPI* 3 *crpI*	220 white

If either *C* or *R* is homozygous in F_1, the resulting F_2 ratio should approximate 9 purple: 3 red: 52 white.

The actual numbers fell between these two theoretical ratios, as is seen from the following comparison:

	Purple	Red	White	Total
Tetrahybrid ratio	66	22	538	626
Observed numbers	75	21	530	626
Trihybrid ratio	88	29	509	626

From the ratio alone it is plainly impossible to say whether the cross in question is a tetrahybrid or a trihybrid. Of course behavior of the reds and purples in F_3 will settle the matter. If, for instance, either *C* or *R* is homozygous, one third of the F_2 red grains should breed true and two thirds produce reds and whites in the ratio of 3:1, while if both are heterozygous, only one ninth of

them should breed true, four ninths produce a 3:1 ratio, and four ninths produce a 9:7 ratio. Similarly, if either one of these two factors is homozygous, of the F_2 purples one ninth should breed true, two ninths give purple and red 3:1, two ninths purple and white 3:1, and four ninths purple, red, and white 9:3:4. But if both factors are heterozygous, out of the twenty-seven F_2 purples only one should breed true; two yield purple and red 3:1; four, purple and white 3:1; four, purple and white 9:7; eight, purple, red and white 9:3:4; and eight, purple, red and white 27:9·28.

The results of intercrossing Tom Thumb pop, Missouri dent and California pop, so far as they are known at present, might be obtained if the three varieties had either of the following sets of formulæ, or any of the modifications of them suggested below:

Tom Thumb pop	*ICRP*		*ICrP*
Missouri dent	*IcRP*	or	*icrP*
California pop	*icrp*		*icRp*

Among the allowable modifications of the above formulæ are these: The formulæ for Tom Thumb pop and California pop may be interchanged. Substitutions of *C* for *R* and *R* for *C* may be made if carried throughout the set. *P* may be present in any one or two varieties and absent from any one or two. Where *I* is present in Missouri dent and also in one of the other varieties, *R* may be present in all three varieties, absent in any one variety, or absent in Missouri dent and either one of the other varieties.